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Woodland caribou persistence and extirpation in relic populations on Lake Superior

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Extended abstract: The hypothesis was proposed that woodland caribou (*Rangifer tarandus caribou*) in North America had declined due to wolf predation and over-hunting rather than from a shortage of winter lichens (Bergerud, 1974). In 1974, two study areas were selected for testing: for the lichen hypothesis, we selected the Slate Islands in Lake Superior (36 km²), a closed canopy forest without terrestrial lichens, wolves, bears, or moose; for the predation hypothesis, we selected the nearby Pukaskwa National Park (PNP) where terrestrial lichens, wolves, bears, and moose were present. Both areas were monitored from 1974 to 2003 (30 years).

The living and dead caribou on the Slates were estimated by the 'King census' strip transect (mean length 108±9.3 km, extremes 22-190, total 3026 km) and the Lincoln Index (mean tagged 45±3.6, extremes 15-78). The mean annual population on the Slate Islands based on the strip transects was 262±22 animals (extremes 104-606), or 7.3/km² (29 years) and from the Lincoln Index 303±64 (extremes 181-482), or 8.4/km² (23 years). These are the highest densities in North America and have persisted at least since 1949 (56 years). Mountain maple (*Acer spicatum*) interacted with caribou density creating a record in its age structure which corroborates persistence at relatively high density from c. 1930. The mean percentage of calves was 14.8±0.34% (20 years) in the fall and 14.1±1.95% (19 years) in late winter. The Slate Islands herd was regulated by the density dependent abundance of summer green foods and fall physical condition rather than density independent arboreal lichen availability and snow depths. Two wolves (1 wolf/150 caribou) crossed to the islands in 1993-94 and reduced two calf cohorts (3 and 4.9 per cent calves) while female adult survival declined from a mean of 82% to 71% and the population declined ≈100 animals.

In PNP, caribou/moose/wolf populations were estimated by aerial surveys (in some years assisted by telemetry). The caribou population estimates ranged from 31 in 1979 to 9 in 2003 ($Y=1267 - 0.628X$, $r=-0.783$, $n=21$, $P<0.01$) and extirpation is forecast in 2018. Animals lived within 3 km of Lake Superior (Bergerud, 1985) with an original density of 0.06/km², similar to many other woodland herds coexisting with wolves (Bergerud, 1992), and 100 times less than the density found on the Slate Islands. The mean moose population was 0.25±0.016/km² and the wolf population averaged 8.5±0.65/1000 km². Late winter calf percentages in PNP averaged 16.2±1.89 (25 years); the population was gradually reduced by winter wolf predation (Bergerud, 1989; 1996). The refuge habitat available is apparently insufficient for persistence in an area where the continuous distribution of woodland caribou is fragmented due to moose exceeding 0.10/km² and thereby supporting wolf densities ≥6.5/1000 km².

A second experimental study was to introduce Slate Island caribou to areas with and without wolves. A release to Bowman Island, where wolves and moose were present, failed due to predation. Bowman Island is adjacent to St. Ignace Island where caribou had persisted into the late 1940s. A second release in 1989 to the mainland in Lake Superior Provincial Park of 39 animals has persisted (<10 animals) because the animals utilize off-shore islands but numbers are also declining. A third release to Montréal Island in 1984 doubled in numbers (up to 20 animals) until Lake Superior froze in 1994 and wolves reached the island. A fourth release was to Michipicoten Island (188 km²) in 1982 where wolves were absent and few lichens were available. This herd increased at $\lambda=1.18$ (8 to ±200, 160 seen 2001) in 19 years. This was the island envisioned for the crucial test of the lichen/predation hypotheses (Bergerud, 1974: p.769).

These studies strongly support the idea that ecosystems without predators are limited bottom-up by food and those with wolves top-down by predation; however the proposed crucial test which has been initiated on Michipicoten Island remains to be completed and there is a limited window of opportunity for unequivocal results.

Key words: alternate prey, Canada, escape habitat, forage abundance, habitat, island biogeography, moose, mountain maple, Ontario, optimal foraging, population regulation, predation, Pukaskwa National Park, refuge habitat, Slate Islands Provincial Park, wolf.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) have recently been assessed (COSEWIC, 2002) as threatened in their Canadian range but there has been an awareness of range reduction for decades prior to this official designation (Cringan, 1956). Caribou conservation in Ontario is highly controversial and extirpation along the receding southern boundary of range remains topical (Schaefer, 2003). The hypothesis was proposed that caribou declined in North America following European settlement from wolf predation and over-hunting (Bergerud, 1974) rather than the widely held view that destruction of winter lichen supplies by fires and over-grazing was the primary cause (Leopold & Darling, 1953; Edwards, 1954; Cringan, 1957; Scotter, 1964; 1967; Klein, 1970). Many biologists emphatically rejected the wolf predation hypothesis. Hence in 1974, we selected two study areas for testing the demographic/food parameters of the hypotheses.

For the lichen hypothesis, we selected the Slate Islands in Lake Superior. On these islands Cringan (1956, 1957) had studied the forage requirements of caribou in 1949. These islands supported a closed canopy forest of birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*); terrestrial lichens were nearly absent. The islands had been logged in the 1930s and a major fire had burned the western one-third of the largest island (Patterson) in 1902. The mammal fauna was limited to 11 species with the red fox (*Vulpes vulpes*) the only terrestrial predator of any potential consequence for woodland caribou.

For the control study, we secured a contract to investigate the caribou in Pukaskwa National Park (PNP). The park had a normal compliment of the boreal mammals including moose (*Alces alces*), wolves (*Canis lupus*), and bears (*Ursus americanus*). We conducted studies at PNP only from 1974 to 1979. In later years the Park staff monitored caribou and moose numbers and measured the recruitment of both species. In PNP about a third of the total area (1878 km²) had been burned in 1931 and 1936 and extensive stands of terrestrial lichens existed in open grown Jack Pine forest (*Pinus banksiana*). In addition, terrestrial lichens were available along the coast on raised bedrock formations ("balds") and arboreal lichens were present on the older conifers on the humid coast. Both areas were originally thought be populated by about 25 caribou in 1974 (Euler *et al.*, 1976; Pukaskwa National Park files - CWS 1972 faunal survey Bruce C. Johnson saw 12 caribou).

This paper provides data on the numbers of caribou in both populations from 1974 to 2003 (30 years). In addition to empirical data to distinguish between the two hypothesis (predation vs. winter lichens), experimental evidence was needed. Hempel (1966: p. 25)

described a *crucial test* to decide between two rival hypothesis as "a decision between the two may be reached if some test outcome can be specified for which H₁ and H₂ predict conflicting outcomes." Bergerud (1974: p. 769) purposed the test of introducing caribou to an island with minimal lichen supplies and later, if the caribou increased, while food supplies were still adequate, introduce wolves; if the herd increases in the absence of wolves H₁ (need lichens) is refuted; if the herd then declines with the wolf introduction H₂ (predation limits) is accepted. In 1982, caribou were introduced to Michipicoten Island south-east of PNP. Michipicoten Island lies in the Great Lakes-St. Lawrence Forest Region (Rowe, 1972), which is primarily a hardwood forest with minimal lichens. Wolves have not been introduced to Michipicoten Island but in the winter of 1993-94 two wolves crossed on the ice to our Slate Island study area at a time when there was adequate forage on the Islands. In other tests of the wolf predation hypothesis versus the lichen hypothesis, caribou from the Slate Islands were introduced to areas where wolves were present (Lake Superior Provincial Park, and Bowman Island adjacent to St. Ignace Island) and where they were absent (Montréal Island).

Pic Island is another site on Lake Superior where an island provides refuge habitat sufficient to anchor a naturally persisting caribou population. Studies carried out on this population (Steve Ferguson, ATB, and RF) have been reported (Ferguson *et al.*, 1988).

Description of the main study areas

Slate Islands

In the northernmost arc of Lake Superior, the Slate Islands are a cluster of 7 significant islands plus islets (36 km²) in the vicinity of Terrace Bay, Ontario (Butler & Bergerud, 1978). Laying almost 9 km off-shore at the closest point, the archipelago lies within a circle roughly 8 km in diameter believed to be the central uplift of a large impact crater (Grieve & Robertson, 1977). Extensive Lake Superior waters in the bays and channels inside the archipelago take on the aspect of inland lakes in sharp contrast to the behaviour of waves and winds on the lake in general.

In most winters Lake Superior does not have complete ice cover but this was seen twice over the thirty years when ice came early and stayed late. In most years, but not all, an ice bridge formed between the Slate Islands and the mainland shore at some time during the winter. When ice does form it is late by the standard of nearby inland lakes, or by the standard of lakes and ponds on the Slate Islands, due to the large thermal mass of the lake. An ice bridge by mid-January would be early and for it to stay past the

first days of March would be late. Such ice bridges are prone to break-up in 24 hours if high winds develop. Given the timing, when ice on Lake Superior is available, it is not well suited to the normal seasonal migration or seasonal dispersal urges of caribou or wolves.

The regression of the start of the growing season 1967 to 1988 was $Y = 248336 - 11.182X$, $r = -0.482$, $n = 22$, $P < 0.05$, Y = Julian date regressed against X = year (last 2 digits). The extrapolated date of green-up in 1967 from this regression line is June 11 and 22 years later in 1988 it had advanced to May 14. The weather station at the light house on the island was closed in 1989 and we were unable to calculate the growing season start in later years. None of the corrections we applied to concomitant statistics 1967-1988 from nearby mainland stations provided a useful extrapolate of growing season dates post 1988 for the islands. The Islands are strongly influenced by a maritime climate.

About 80% of the Slate Islands shows evidence of being burned in the late 1800s in one fire event. The western half of Mortimer Island (second largest) was burned earlier, with forest cover composition similar to other areas but advanced in age structure by possibly up to three decades. Two small decadent white birch (*Betula papyrifera*) stands, with open canopies and raspberry (*Rubus strigosus*) understory, on Patterson Island (the largest), were aged to 130-150 years old in 1978. The south-western third of Patterson Island (largest) was re-burned in 1902. Horse logging for conifer pulp, evident in 1949 aerial photographs, in the 1930s was widely distributed with a concentration of activity in the lowland areas which may not have been so affected by the forest fires. Logging in the late-1800s is also said to have taken place (Cringan, 1956).

The Slate Islands forest canopy was classified based on standard 1:15 840 B&W provincial aerial photographs from 1949 and 1974. These included: (1) lakes and ponds (there are 30) 3.3% of the area, (2) meadow (sedge/grass areas) <1% trace in both 1949 and 1974, (3) alder 5.1% 1949 and 1.9% 1974, (4) birch overstory 38.0% in 1949 and decreasing to 14.0% 1974 (5) birch-fir (*Abies balsamea*) (birch dominant) 36.1% 1949 increasing to 48.5% 1974 (6) fir-birch (fir dominant) 8.7% in 1949 and 21.1% in 1974, (7) lichen-bedrock (supporting *Cladonia* lichens) 1.3% in 1949 and 1.4% 1974 (8) conifer-feathermoss 3.6% 1949 and 5.8% 1974, (mostly fir dominant and rarely pure black spruce (*Picea mariana*)) (9) conifer-sphagnum 3.9% 1949 and still 3.9% in 1974 (black spruce dominant but with a surprising number of overstory fir occurring, sometimes white cedar (*Thuja occidentalis*) dominant). The

well-drained upland sites were notable for the presence of scattered large white spruce (*Picea glauca*) and they highlighted the skyline. Large white cedar also occurred on upland sites which were very steep and very fresh. Arboreal lichens were present on all tree species with variation by tree species and branch age in lichen species assemblage and quantity supported.

The herbivores competing with caribou on the Slate Islands for terrestrial forage were beaver (*Castor canadensis*), and snowshoe hares (*Lepus americanus*). Beaver impounded water for lodge building opportunities and access to forage in highly unlikely drainages, in addition to normal dam building and site occupation, and so achieved foraging access more widely than expected for similar habitats with predators present. Beaver accelerate succession to conifer overstory after canopy disturbances and deciduous species regeneration in proximity to waters they occupy, and on the Slate Islands this influence was more extensive than normal.

Pukaskwa National Park

Pukaskwa National Park occupies 1878 km² of the Central Boreal Uplands (Poitevin, 1989) and stretches for about 80 km along the north shore of Lake Superior, where due to a prominent jog southward the shoreline is oriented north-south in the park. The park has rugged terrain and many rivers; the largest happen to be on the northern and southern boundaries: respectively the White River and Pukaskwa River. The Swallow and Cascade Rivers are located midway down the shore and along with the Pukaskwa are travel routes for wolves to reach the Lake Superior shore.

Approximately 25% of PNP was burned in 1931 and 1936 and part of the 1936 burn regenerated with an extensive *Cladonia* cryptogam near the shore at Oiseau Bay. Extensive stands of terrestrial lichens existed in open grown jack pine forest (*Pinus banksiana*). In addition, terrestrial lichens were available along the Lake Superior near-shore on bedrock outcrops and arboreal lichens were present in the conifers. PNP, in contrast to the Slate Islands, has both an abundance of arboreal lichens within reach of the animals and the extensive lichens in old burns and on bedrock outcrops. Although the effect has not been quantified, it is presumed that the proximity to maritime climatic effects from Lake Superior, at both PNP and the Slate Islands, is favourable for arboreal lichen growth.

In the early years of our research, the caribou occupied the shorelands south from the Willow River with a concentration using the islands near Oiseau Bay. The distribution continued along the shore south to the Pukaskwa River and then east of the Park

along the shore to Floating Heart Bay 26 km to the east along the shore (Bergerud & Dalton, 1990). In latter years, the herd has concentrated in the vicinity of Otter Island (south of the Cascade River) which is the major calving, rutting, and meeting location. The caribou in the past have made long movements but always stayed near the Lake Superior shore (Bergerud, 1985: Fig.1; Bergerud, 1989). One animal tagged on the Slate Islands did reach PNP during this study (Bergerud, 1989). This male would have traveled the near-shore past Pic Island and the town of Marathon.

Methods

Studies of varied intensity and kind were carried out at the Slate Islands and Pukaskwa National Park from 1974 through 2004. The methods reported below are only those relevant to the results reported and only in as much detail as required by the weight of its use.

Slate Islands floral studies

By 1979, we had established 6 moderately large exclosures (total area = 152 m²) distributed in the 5 major forest canopy classes. Throughout the study, we made comparisons of the availability of green foods inside and adjacent to the large exclosures. Each spring in May, we weighed the lichen litter that had accumulated in these exclosures in the previous 12 months and included lichens on trees that fell within the exclosures that would have fallen within reach of caribou. Also from 1979 to 1998, we annually monitored survey lines to measure the DBH of conifers that had fallen over the trail since the previous tally. The lines were 3.3 km in length 1979-1991 and 1.7 km 1992-1998.

The growth habit of mountain maple on the Slate Islands was unusual and it was recognized that browsing may have heavily influenced this species. It was possible that a historical record of caribou population dynamics might be recorded in the age structure of stems. The age distribution of mountain maple stems was sampled in four stands. Destructive sampling of all maple stems within 10 m of a point in the interior of stands with a continuous sub-canopy of maple obtained stem 'cookies' for age analysis. Cookies (20 cm long) were taken at 0.5 m or less stem height. Stems with butt rot were sampled at the lowest height that presented a solid core suitable for aging, and age was adjusted. Ring counts were read (WJD) at two locations on each cookie with a hand lens after preparation with a thin and sharp utility knife blade, and a third if the counts disagreed. The frequency distribution of the aged stems was smoothed by generating forward and backward 3-year running

averages of frequencies and taking the mean for each year, to address age assignment errors.

Foraging on shrubs and herbs was evaluated in 1985.

Slate Islands faunal studies

The population size of Slate Island caribou was estimated all years 1974 to 2003 with a walked strip transect survey (King, 1937), commonly referred to as a *King census*. Caribou tagging was initiated in 1975 and the tag-recapture (sightings) Lincoln Index (Lincoln, 1930) population estimate was calculated for 1975 to 1997.

The captures were based on baited salt traps (2-4 traps), boat herding to drive-traps at water crossings (2), a walk-through travel route trap, occasional use of drop-nets, and from boats for swimming caribou. There were 628 capture events. The main capture effort was usually conducted in the fall. We were able to capture any swimming animals encountered regardless of size and stage of the fall rut and the traps being open and set for automatic capture were similarly unbiased.

A trap card was filed for each capture event noting the date and time, location/method, capture crew, processing leader, animal sex, presence of udder, sighting and capture of calf and calf tags, body measurements, tags removed and applied, blood samples collected, fecal sample collected, weight, incisor wear, and the incisor collected for aging. Animal care protocols were maintained and animal stress parameters monitored (body temperature, respirations, exertion).

For tagging, at the outset of studies we used individually unique colour combinations of sewn vinyl ear tags (applied with numbered metal ear clips through a grommet) and collars; after c. 1978 we transitioned to numbered large cattle ear tags with colour combinations unique by male or female, and phased out collars.

There were tags in all segments of the population but there were probably tagging biases: males used water crossings more than females in the breeding season, swimming cows and their calves were selected prior to other animals available in the water at the same time, trap vulnerability bias could not be assessed, and selective spring and summer trapping effort avoided adult males and animals with antlers in velvet to avoid overheating and injuries respectively.

The mean tagged animals available each year (1975 to 1997) was 44 ± 4.04 , $n=23$ (unpubl. data). We did not observe any animals that had lost one or both tags based on only a single tag or a split ear in the 4-year interval post-tagging. We were able to see most animals, at least occasionally, at a salt lick established centrally on Patterson Island (the largest - 23 km²). A second salt lick was established on Mortimer Island

(second largest - 8 km²) and monitored for a number of years to test if animals on Mortimer were infrequent visitors to Patterson Island. The survival of individual tagged animals was based on the last year an animal was seen, after waiting 3 additional years to decide if the animals had been overlooked. If an animal was later seen with tags in good condition they were added back to the tagged pool. Recaptures were re-tagged with fresh tags when a couple years had passed.

The requirement for either random tagging or random recapture for a valid capture-recapture population estimate was met with sighting effort, not capture effort. Sightings included in the Lincoln Index for the yearly estimates included all sightings from May and June: casual encounters, strip transect sightings, and salt lick observations.

King census strip transects were walked by single persons on compass courses with minimal deviation from straight lines, in forestry timber cruising compass-man style. Transects were walked at a normal walking pace, excepting required frequent stops for compass bearing taking for route extensions; as such, noise levels were moderate and approximated observed noise levels of individual caribou travelling with a mind to get somewhere. The strip transect routes were chosen for practical turning points (topographic features, lakes, bays or points, etc.), and boat drop-off and pick-ups. Routes were selected to avoid areas disturbed in recent days and with the goal to have maximal line dispersal for the level of total effort invested. Traverses were walked in May and June, with a majority in May before calving and green-up in most years, on days with little or no wind, and with the ground litter preferably damp; observing these conditions, calling for relatively good listening conditions, standardizes the expectation for flushing distance variability and is the rational for the parametric statistical assumptions.

Observers determined the length of their pace and paced the line-of-sight distance to the flushing location of caribou seen or heard. Distances to dead caribou located and snowshoe hares observed flushing were also recorded. Notes were taken on the condition of carcasses and a decision made whether it had died in the previous winter or in previous years. The definition of a valid previously unfound mortality was that the skull and/or mandible were found and collected. Without major predators, the bones generally were not strewn widely, and skulls and long bones were intact. In the early years, visibility under the forest canopy was excellent because of the elimination of deciduous browse by the caribou and the lack of deadfalls and fewer regenerating balsam fir thickets. As the study progressed, the area of blown down interlaced trees and of regenerating fir 'thicker' accumulated; average

visibility declined and it was harder to listen for or see flushed animals.

For each strip transect flush, the observer filed a data card including map location, habitat, flush distance and angle from transect, behaviours, ears observed and tags seen, and if a valid view of the rear for sex determination and udder condition was accomplished.

The mean annual flushing distance of 33.3 ± 1.12 m (30 years) was not significantly longer in 1994, 29.8 m and 1995, 27.4 m, when wolves were present. The mean distance walked per year was 99.5 ± 9.05 km, the mean caribou seen per strip transect survey was 45 ± 5 , or the caribou per km walked was 0.48 ± 0.038 (1974-2003, $n=30$). The mean area annually searched was 6.4 ± 0.55 km², 18% of the archipelago.

To determine which population estimate method (*King census* or Lincoln Index) was the best predictor of population change, we calculated an independent method of change by demographic statistics (unpublished analysis); the predicted percent change Y1 to Y2 was 100 minus the survival rate Y1 + annual recruitment (R1). The mean annual change in numbers based on demography from 1980-81 to 1995-96, $16 \pm 4.9\%$. In comparison, the percent change based on the *King census* estimate was 38 ± 9.2 (a perpendicular sighting distance was more deviant). For the Lincoln index, the per cent annual change was $22 \pm 3.4\%$ and we felt it was the more reliable method, although there were years the strip transects were closer to the percent change based on demography. The correlation between the annual totals of the *King census* and the Lincoln Index estimates was significant ($r=0.717$, $n=23$ years, $df=21$, $P<0.01$).

We established a defection rate for interpreting winter pellet survey data: pellet survey counts were conducted in 7 years of the study with tally on 2 m X 20 m segments of continuous transects through proportionately representative forest communities. Captive Slate Island caribou were kept at Thunder Bay and the winter defection rate of 23 pellet groups/day was estimated (unpubl. data).

When we arrived on the Slates in 1974, we were surprised to find a number of adult males without visible antlers (hummels). Also few of the females had antlers. Also in 1974, we encountered small animals the size of yearlings but who had the long face of an adult. Hence we only felt confident in expressing recruitment as the calf percentage of total animals rather than the more rigorous calves/100 females' index.

In 16 years, a brief period of study in March (late winter) was done to measure snow depths, locate carcasses for indications of die-off, observe foraging behaviours in die-off and non-die-off years, and compile age and sex composition tallies based on track

and sign characteristics. Usually with a crew of 4+, only about 10-20 caribou per trip were seen each trip, and the animals appeared to be relatively inactive. Winter classification tallies depended on sign reading: calves separated from adults based on track size and males distinguished from females on the location of the urine spot before or behind the rear tracks and the position of the rear feet based on the drag and spread of the tracks.

Dropped antlers, old or new, on the Slate Islands were almost wholly undamaged by gnawing. Gnawing on cast antlers is a phenomenon that is ubiquitous elsewhere (we surmise that the absence of any squirrels in the fauna may explain this). In all years, dropped antlers were collected and segregated into ten classes on the basis of weathering (applies to antlers found under full forest canopy cover), and were measured and weighed. The oldest, class 1, had shell-like points gone soft, were cracked and partially buried by mosses and humus. One antler was under the humus that had accumulated since the 1902 burn (assessment by forest fire expert Dr. M. L. Heinselman). Class 10 antlers still had rich brown pigment on both surfaces and had been shed the previous fall. This class was based on comparison with antlers known to have been shed the previous winter since they were found in the baited traps left open the previous autumn. The pedicle size on the skulls of males that died in the winter was compared to the mean size of the antler burrs of class 10 antlers from the previous year to quantify whether large antlered males were more susceptible to starvation than smaller males.

An apparent salt lick had existed at Mud Lake in the center of Patterson Island in 1949 (Cringan, 1956). We started placing salt there in 1976 and made daily observations mostly in June during the study. All animals were classified including the sex of young calves. The udders of females were classified as to size to judge for barrenness in that year, the likelihood of a calf having been lost earlier (medium to small regressing udder), and the probability of the calf being nearby but unobserved (extended udder), or with calf present and the likelihood that the cow is the mother. The length of antlers was estimated using ear length as a scalar of height. Physical condition was assessed on a 10 point yes/no system (i.e. ribs showing yes or no etc.) (Bergerud, 2001: Fig. 27) and molt patterns drawn to further recognize untagged animals revisiting salt licks within the day or on following days.

Pukaskwa National Park faunal studies

The PNP caribou population was surveyed in most years following a new snowfall in March. We participated from 1974-79, and in later years the survey was made solely by park staff. The surveys were attempts at complete counts in a 5 km strip adjacent to Lake

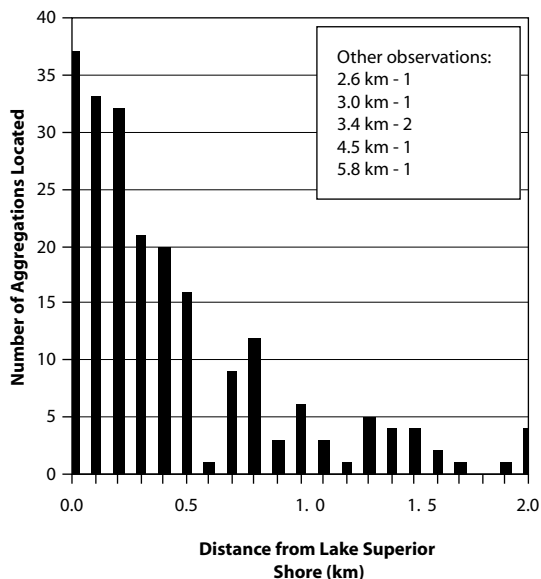


Fig. 1. Puckaskwa National Park caribou live within 1-2 km of the Lake Superior shoreline based on population surveys 1974-1988.

Superior for the whole north-south extent of the park, and sometimes further east along the shore. Surveys for moose and wolves and radio-tracking of caribou described a very low incidence of caribou forays away from the Lake Superior shore.

Caribou survey lines were flown by helicopter parallel to the shore and were more closely spaced near the shore; 97% of the tracks were within 2 km of Lake Superior (Fig. 1). The interior of PNP has the greatest snow depths in Ontario (Finlay, 1973) but is reduced along the shore. On the surveys, fresh caribou tracks were tallied and separated from moose relative to habitat locations and sinking/drag track characteristics. Caribou commonly visited small lakes digging holes for slush and these networks of tracks and holes, called spider webs (Simkin, 1965), were investigated by landings for individual counts and calf/adult male/female segregations. Clearly these were minimum counts. Additionally the radio tracking of animals captured on Otter Island showed that animals did not always remain in PNP but would travel the near-shore as far as 30 km farther east along the shore to Floating Heart Bay (Bergerud & Dalton, 1990; Neale, 2000: p45) and possibly a like distance northwest along the near-shore to Pic Island. Otter Island in Lake Superior (Bergerud, 1985: Fig. 2) is centered north-south in PNP and presented a significant opportunity for low predation risk rutting and calving (1.9 km² and 0.5 km offshore).

The moose were counted in winter surveys following a fresh snowfall in 1975, 1976, 1977, 1979, 1984,

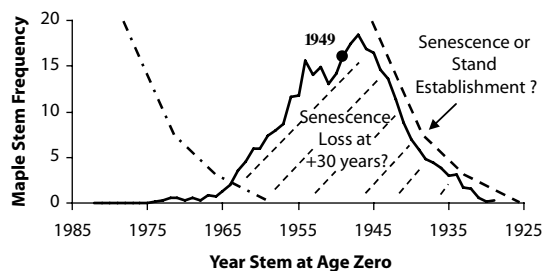


Fig. 2. Mountain maple (*Acer spicatum*) ages ($n=318$ stems) were sampled in four stands on the Slate Islands. Ages were smoothed assuming ± 3 years variability in accuracy of ring counts. Cringan (1956) measured the plant communities in 1949. The oldest stems were aged to initiation in 1929, the youngest to initiation in 1972. The shape of the frequency curve for stems initiated 1929 to 1947 suggested that natural senescence may be acting on the population of stems. Given no new recruits post-1974, and advancing senescence by 30 years would suggest the maple stem population should be nearly completely collapsed. While senescence was obvious post-1990-95, ocular estimates of the collapse under way and the rarity of observed dead sub-canopy maple stems in the stands 1975-85 do not suggest it is proceeding this fast, possibly at half this rate $\pm 15\%$; suggesting in turn that maple understorey stand establishment is actually described by this age structure.

1986, 1990, 1993, 1996, and 1999 (Bergerud *et al.*, 1983; Burrows, 2001). The counts 1975-79 involved strip transect methods (see Bergerud *et al.*, 1983) while later workers switched to the Gasaway block method (Gasaway *et al.*, 1986) with some additional modifications. Also, the counts in the 1970's were limited to PNP proper (1878 km²) while some later counts enlarged the area to the Greater Pukaskwa Ecosystem, 10 000 km² (Burrows, 2001).

The wolf population was estimated in 1977, 1978, 1985, 1987, 1990, 1996, 1997, and 1998. These estimates were not very accurate and generally made in conjunction with moose surveys. Further those in the 1970s-80s were limited to PNP whereas several packs were on the boundary of the park and their total home ranges were not documented. The most accurate work was done in the 1990s (1994-99) during the Greater Pukaskwa Ecosystem studies when wolves were radio tracked (Burrows *et al.*, 1996; Forshner, 2000).

Caribou introductions

Caribou from the Slate Islands were released into areas with and without wolves. The introduction areas with wolves and moose were Lake Superior Provincial

Park (1989) and Bowman Island (1985) (white-tailed deer also present) immediately adjacent to St. Ignace Island. Caribou were still present on St. Ignace in the 1940's (de Vos & Peterson, 1951). The introductions to islands without wolves or moose were: Montréal Island (1984), and Michipicoten Island (1983).

Results

Slate Islands forage resources

In June 1974, ATB & HB landed on Patterson Island for the first time and were astonished at the heavy environmental footprint of the caribou; trails led everywhere. The first impressions were that the forests were missing a shrub understory and that the arboreal lichens on conifer branches and deciduous tree trunks were browsed in the fashion of a white cedar (*Thuja occidentalis*) browse line in white-tailed deer (*Odocoileus virginianus*) wintering yards; a browse line was also evident for foliose lichens on cliff faces.

The best example of the missing understory shrubs was mountain maple whose form was altered from the norm for the area. Maple was not missing, it was present in suitable moisture and nutrient regime sites as expected. Foraging on maple was sufficient though that there was cropping of all suckering stems at the base of maple clumps. This was allowing apical dominance to remain in the stems that had reached into the forest sub-canopy in the past, so these stems were of unusually large diameter and height, and still growing. The area at the base of maple clumps, through the 1970s and to the mid-80s, had the appearance of tended and vigorous gardens with a 1-1.5 m diameter circle of high density maple suckers less than 40 cm tall. During the 1980s, the height which the suckers attained in a year was progressively less and the apparent vigour of the sucker gardens was noticeably less as the area covered at the base of maple clumps decreased. The record of browsing intensity in the maple was assayed by obtaining ages of mountain maple from four stands sampled ($n=318$) (Fig. 2): 1978 – 2 stands, 96 & 101 stems; 1982 – 2 stands, 50 & 71 stems. The oldest maples were two stems dated as becoming established in 1929; the youngest were 4 stems established in 1971 or 1972. In 1949, at the time Cringan (1956, 1957) conducted vegetation and browsing studies, the sampled stands had stems in the sub-canopy as is seen today, but also a steady, if low, recruitment of stems into the canopy.

Over the course of the study, and accelerating with time, the once vigorous stands of mountain maple commenced dying without replacement due to butt rot induced vulnerability to wind breakage. Winds also took a toll on mountain ash. This occurred in the birch and fir communities where mountain ash was

Table 1. Comparison of upland forage plant species importance (proportion of biomass in diet) to caribou in 1949 in descending order of importance (Cringan, 1956, 1957) versus 1985.

Winter Shrubs	1949	1985(%)
<i>Acer spicatum</i>	1st	N.A. ¹
<i>Sorbus decora</i>	2nd	N.A.
<i>Salix</i> spp.	3rd	N.A.
<i>Cornus stolonifera</i>	4th	²
<i>Viburnum edule</i>	5th	N.A.
<i>Sambucus pubens</i>	6th	³
<i>Taxus canadensis</i>	7th	N.A.
Summer Shrubs	1949	1985(%)
<i>Viburnum edule</i>	1st	N.A.
<i>Sobus decora</i>	2nd	6th ⁴
<i>Acer spicatum</i>	3rd	4th ⁴
<i>Diervilla lonicera</i>	4th	N.A.
<i>Populus tremuloides</i>	5th	3rd
<i>Rubus parviflorus</i>	6th	1st ⁵
<i>Sambucus pubens</i>	7th	7th
Summer Herbs	1949	1985(%)
<i>Aster macrophyllus</i>	1st	1st ⁶
<i>Aralia nudicaulis</i>	2nd	8th
<i>Epilobium angustifolium</i>	3rd	N.A.
ferns	4th	2nd ⁷
<i>Clintonia borealis</i>	5th	N.A. ⁸
<i>Cornus canadensis</i>	6th	3rd
<i>Linnaea borealis</i>	7th	N.A. ⁹

¹ N.A. - Not available.

² *C. stolonifera* was still present in 1985 in typical shrub form, but winter browsing was not evident, and was not preferred as summer browse (5th in importance).

³ *S. pubens* was the most common shrub in 1985, but not winter browsed and avoided as summer browse.

⁴ Available only as sprouts not as shrubs.

⁵ By c.1990 *R. parviflorus* was N.A.

⁶ The growth habit of *A. macrophyllus* was progressing towards a diminutive form by the early 1990's. In the late 1970's the only foraging impact noticeable was heavy early spring use which delayed the date of full ground coverage where it occurred.

⁷ Based on *Dryopteris spinulosa*, other ferns also still available.

⁸ *C. borealis* was available as forage in plots measured 1977-1980.

⁹ *L. borealis* was still present in 1985 but mostly in wetter habitats.

Note: Three species: *A. macrophyllus*, *D. spinulosa*, and *R. parviflorus* made up 63% of the summer forage available in 1985.

Table 2. Comparison of the green phytomass of utilized plant species in the 6 large exclosures (total 151 m²) based on 10 m² inside and 10 m² adjacent outside per enclosure May and June 1994.

Dates ¹	Exclosure	Dry Grams per m ²		
		Deciduous Shrubs	Herbaceous	<i>Taxus canadensis</i>
May 17 - 24	Inside	16.1	15.0	1320.0
	Outside	0.2	3.6	0.0
	Difference	-99%	-76%	-100%
May 26 - June 1	Inside	4.0	9.6	43.8
	Outside	0.2	2.0	0.7
	Difference	-95%	-79%	-98%
June 10 - 14	Inside	9.1	13.8	255.0
	Outside	1.0	2.5	0.0
	Difference	-89%	-82%	-100%

¹ New quadrats selected each period.

Table 3. The comparison of herbaceous phytomass of the nearby Leadman Islands (4 m² summed) and the Slate Islands (221 m² summed) measured in 1985.

Plant Species	Slate Islands (gms in 221 m ²)	Leadman Islands (gms in 4 m ²)	Leadmans > Slates (factor ¹)
<i>Roseus streptopus</i>	1.1	7.2	362
<i>Rubus strigosus</i>	97.5	2.2	1
<i>Clintonia borealis</i>	7.6	22.8	166
<i>Maianthemum canadense</i>	51.6	17.3	19
<i>Oxalis montana</i>	8.4	6.4	42
<i>Dryopteris spinulosa</i>	159.9	329.6	114
<i>Ribes glandulosum</i>	161.3	36.2	12
<i>Sorbus decora</i>	10.4	17.3	92
<i>Aralia nudicaulis</i>	2.4	10.2	235

¹ e.g. (7.2/4)/(1.1/221) = 362X. These results are conservative since caribou sometimes reach the Leadmans and additionally there was a major caribou die-off on the Slate Islands in 1984-85.

Table 4. Caribou forage species at or near functional extirpation from the Slate Islands but still present or re-appearing in the large exclosures in 1985.

Plant Species	Grams Inside (28 m ²)	Grams Outside (28 m ²)	%Gone
<i>Actaea rubra</i>	29.7	0.3	99%
<i>Athyrium felix-femia</i>	76.2	0.0	100%
<i>Botrychium lunaria</i>	0.8	0.0	100%
<i>Taxus canadensis</i>	41.4	0.9	98%
<i>Goodyera repens</i>	2.4	0.0	100%
<i>Gautheria hispidula</i>	30.9	1.1	96%
<i>Listera chordata</i>	0.3	0.1	67%
<i>Coptis groenlandica</i>	1.2	0.1	92%
<i>Amelanchier sanguinea</i>	0.1	0.0	100%
<i>Aralia nudicaulis</i>	0.3	0.0	100%
<i>Populus tremuloides</i>	0.5	0.0	100%
<i>Taraxa cumofficinale</i>	0.1	0.0	100%
<i>Rosa acicularis</i>	14.8	1.3	91%
<i>Roseus streptopus</i>	5.5	0.7	87%

present as scattered stems and butt rot was common, and it also occurred in the few stands where mountain ash was the dominant or co-dominant cover. The latter stands tended to occur on shallow soils over fragile bedrock or raised beaches where mountain ash was not wind-firm at mature sizes.

The aspen was also gradually reduced to very low occurrence levels during the 30 years; that is, since the beaver population was extremely high (originally at 1 colony per km²), and they foraged at abnormal distances from water to seek aspen stems.

The analysis of forest cover composition indicated that balsam fir had increased from 1949 to 1974 and this succession continued through our 30 year study. Normal secondary succession in the boreal forest, if and when forest fires do not restart primary succession directly, is replacement of deciduous and coniferous shade intolerant pioneering species with shade tolerant coniferous species. Additionally, the vegetation survey documented functional extirpation of a number of the summer forage species that were most heavily foraged in 1949 (Table 1); several others were on the verge (Tables 1 to 4). By functional extirpation we mean that the plant was still present and vigorous in natural caribou browsing refuges but was no longer available in reach of caribou, or it was present in reach but only in a non-flowering vegetative form that was diminutive

Table 5. The arboreal lichen litter measured and removed each spring from the large exclosures compared 1979-81 versus 1989-98.

Year	Forest Cover Type		Size of Excl. (m ²)	Mean per Year		Island-wide mean annual lichen litter-fall (kg)
	Name	Island-wide Area (ha)		gm per Excl.	gm per m ²	
1979-88 ¹	Birch Overstory	494	37.5	5±2	0.13	642
	Fir-Birch	245	29.1	9±1	0.30	735
	Fir-Feathermoss	206	18.3	108±18	5.90	12 154
	Birch-Fir	1714	38.6	53±8	1.37	39 079
	Birch-Fir	above	28.8	92±15	3.19	above ³
	Spruce-Sphagnum	139	17.8	13±5	0.73	1015
	Totals and Means	3298	151.8	46.6	1.90	53 625
1989-98 ²	Birch Overstory	494	37.5	47±11	1.26	6
	Fir-Birch	245	29.1	55±15	1.89	5
	Fir-Feathermoss	206	18.3	218±27	11.90	25 514
	Birch-Fir	1,714	38.6	116±27	3.01	62 047
	Birch-Fir	above	28.8	122±18	4.23	above ³
	Spruce-Sphagnum	139	17.8	77±29	4.32	6005
	Totals and Means	3298	151.8	105.8	4.43	104 421

¹ The estimated arboreal lichen litter 53 625 kg equals 117 975 lbs. In Nfld. caribou ate 10 lbs. per day or 210 days equals 117 975/210 equals a carrying capacity of 56 animals.

² The estimated arboreal lichen litter 104 421 kg equals 229 726 lbs. divided by 2100 lbs. per animal equals a carrying capacity of 109 animals.

³ For the two exclosures in Birch-Fir the mean gms/m² was used in calculating kg available.

as compared with its normal form contemporarily on the adjacent mainland, and assumedly with 1949 since this phenomenon was not noted at that time (Cringan, 1956). The most dramatic example of the former was bush honeysuckle (*Diervilla lonicera*) which, while being perennial, does not extend a clone bearing root system and does not have a vegetative form that stays close to the ground. A good example of the latter was clintonia (*Clintonia borealis*) which was ubiquitous in its' normal range of preferred sites but at very low density and was evident above ground with single 10 cm or less leaves; plants persisting in this manner were always part of an extensive clonal root system.

The terrestrial lichen community was found on raised bedrock but covered only 0.5 km² and existed only as fragmented podetons that would contribute little to the diet. In 1981, we measured the phytomass

of this lichen community on the Slates by weighing the lichen phytomass that we could pick in 5 minutes in each of 20 m² random quadrats. The yield from these *in situ* quadrats averaged 3.15±0.32 gm. For a control we picked 20 m² quadrats on the mainland immediately adjacent the Slate Islands. There the mean phytomass picked in 5 minutes averaged 173.5±28.57 gm (55 times greater). The terrestrial lichen on the Slates was less than 1 cm in height and picked from within cracks in the bedrock or it was sparsely present in clumps of feathermoss or other ground-hugging mosses. This being little changed since 1949, although Cringan (1956) estimated the difference between mainland lichen and the Slate Islands in the order of 20 times greater, and this may be the clearest indication that there was actually more lichen available in 1949. That is, in the absence of 1949 biomass measurements the reported occurrence, cover, and a qualitative description of condition might also describe the condition post-1974. Terrestrial lichen on the mainland was of a normal 10 cm or so in height and 'rooted' in an organic mat of rotting lichen.

The arboreal lichen phytomass available to caribou, on branch litterfall and on blown down tress, measured in the 6 large exclosures in 19 years (1979 to 1998 broken) increased through time as the conifer forest aged (Table 5) ($Y = -20.474 + 0.266X$, $r=0.770$, $df=17$, $P<0.01$). In the early years, it might have provided biomass sufficient for 50 caribou and while in the later years of the study it was estimated to be sufficient to support 100 animals (Table 5).

Slate Islands population demography

The first *King census* strip transect estimate in 1974 was 140 animals, much greater than the estimate that had been repeated over the years of ~25. Another crew that visited the island (Euler *et al.*, 1976) quantified winter pellets to evaluate habitat preferences. Our re-analysis of their pellet count data using our habitat classification, gave a population estimate of 177. We also found dead caribou as did the other team. The estimation from the previous winter's carcass survey in the spring of 1974 was that 194 animals had died. The population the previous fall had exceeded 300 animals or 9+ animals per km².

For the next 23 years (1975 to 1997), the population fluctuated between 200 and 500 animals based on the Lincoln Index or from 5.0 to 12.3 caribou/km²; or based on the strip transects 1974 to 2003, from 100 to 600 or 2.9 to 16.9/km² (Fig 3). The percentage of calves in the fall varied from 3 to 25% 1974-98 (excluding 1994 and 1995) and averaged 16.0±0.93%, $n=18$ years, mean sample size 125 (Fig. 3). Recruitment was much less for the 1994 and 1995 cohorts when wolves were present. The fall count in 1994 was 3.0%,

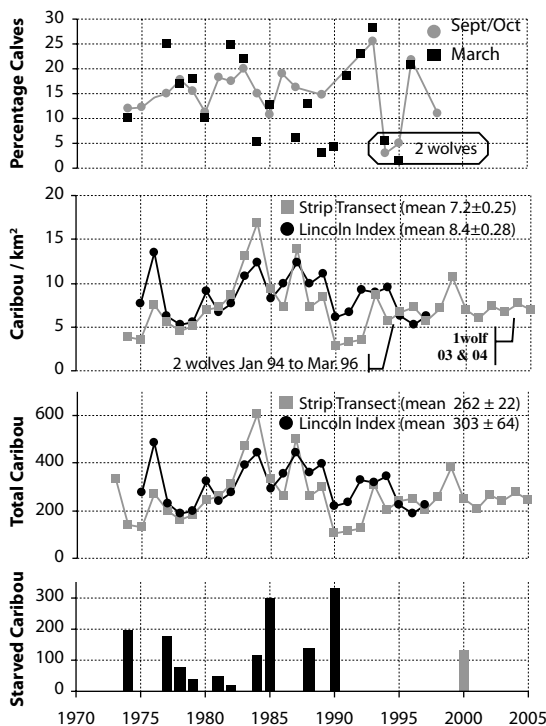


Fig. 3. The demographic parameters of the caribou on the Slate Islands 1974 to 2005. Starved caribou from spring strip transect surveys. Total caribou 1973 is backcast from 1974 sum of starved and living estimates. Total caribou in 1999 and 2000 based on less than 30 km of strip transect per year, however it was walked by a single experienced observer (L. C.); variation in estimates wider than the rest of the series. Starved caribou estimate in 2000 based on difference in total caribou estimates 1999 to 2000, no carcasses located (grey bar).

$n=166$ and in 1995, 4.9%, $n=122$. The mean winter percentage in March (excluding the 1994 and 1995 cohorts) was 15.4 ± 1.95 (17 years, mean sample size 123). The percentage calves in March 1995 and 1996 with wolves was 5.4, $n=165$ and 1996 1.5, $n=129$ (not significantly different than in the fall). The greater variability in the winter percentages (SE 1.95) resulted since calves were already reduced in the winters of major die-off by the time we arrived, 1984-85 5.2% ($n=191$), 1986-87 6.1%, ($n=331$) 1989-90 3.0% ($n=135$). Some demographic parameters of general interest are listed (Table 6).

Based on the pellet count Cringan (1956) made in 1949, and our forest cover stratification for that period, we recalculated and got a similar (Cringan, pers. comm.) high figure of 150 animals using our methods. Seven pellet counts from 1978 to 1983 provided mean estimates 262 ± 23 animals similar to the Lincoln Index for the same period, 285 ± 37 animals. The pellet method provided an approximation of numbers but was not sufficiently accurate to predict annual changes. However, it adds cause to believe the population has probably fluctuated from 100 animals to 500+ at least since 1949.

There was an almost complete natality failure in 1990. Many pregnant cows had died prior to parturition in the winter of 1989-90. The survival rate 1989-90 for tagged females was only 15% (4 of 26) and males 12% (2 of 17). Additionally, we found the legs of newborn calves that spring at two active fox dens and the hooves of the neonates showed no wear; the newborns were either born dead or never stood. We had no 1990 fall count but the 1990-91 winter percentage of calves was 4.2% ($n=118$).

The parous percentage for tagged females was 61.7 ± 3.30 in 19 years (mean sample 19) and was consistently higher than that of the larger samples of untagged females that included more pre-puberty animals, $59 \pm 3.12\%$ (19 years, mean sample 169). But there were exceptions to the low rates; in 1986, the parous percentage of tagged females was 71.4% ($n=28$), and 76.6% for untagged females ($n=286$), and in 1991 tagged females were 78.6% parous ($n=14$) and, untagged 79.8% ($n=168$). The relationship of the percentage of parous females in the spring (excluding calves of the previous year only), with the weight of captured females (inclusive of long yearlings) the previous fall was significant ($r=0.5193$, $df=13$, $P<0.05$) (Fig. 4).

The mean annual survival rate of tagged females was 82% (383/465, 16 years) and the year with the lowest survival, mentioned previously for 1989-90, was 15.4% for females and 12.2% for males. The second lowest annual survival rate for females was in 1994-95 when wolves were present 71% (24/34).

Table 6. Some demographic parameters from the Slate Islands

Survival Rates of Adults¹

Females:

Years no wolves (excludes 1988-89) $89 \pm 1.67\%$, $n=13$ years, (334/379)= 88%
Years with wolves 1994 71% (24/34), 1995 81% (21/26)
The worst winter die-off 1989-90 15% (4/26)²

Males:

Years no wolves (excludes 1988-89). 84 ± 2.62 $n=13$ years (254/306)=83%
Years with wolves 1994, 87% 33/38, 1995, 91% 52/57
The worst winter die-off 1989-90 12% (2/17)

Mean Pregnancy/Parous Rates (1978 to 1998 with 2 years missing)

Tagged 61.7 ± 3.30 (mean sample size 19), minimum 33.6 (1990), maximum 82.4% (1989)
Untagged 54.9 ± 3.12 (mean sample size 169), minimum 29.8 (1990), maximum 79.8% (1991)

Percent Male Calves

Years no wolves $54.7 \pm 2.37\%$ ($n=16$ years)
Years with wolves 1994 and 1995, 3% and 5% respectively

Percent Adult Males at Salt Lick (1974 to 1996, broken series $n=16$ years)

33.5 ± 2.35 ($n=16$ years) (mean sample 259.6)
Significantly more males in wolf yrs 52.9 (1994), 56.8 (1995) (in forest also)

Percent Calves in Fall (1974-1998, broken series $n=18$ years)

Years no wolves 17.8 ± 1.18 , minimum 15.0 $n=10$, maximum 25.4 $n=63$, mean sample 127.2
Years with wolves 4.0 ± 0.95 sample 1994 166, sample 1995, 122

Percent Calves in March (1974 to 1996, broken series $n=18$ years)

Years no wolves 15.4 ± 1.95 $n=16$, winters of major calf loss 1984 cohort 5.2, 1988 6.1, 1989 3.0, a natality failure 1990 only 4.2 calves because pregnant females died in the major die-off and also calves carried to term were stillborn or never stood, since tiny hooves with no wear found at two fox dens

¹ Based on survival of animals tagged from four cohorts and followed for four years.

² 15% 4 of 26 live: no captures 1986, 1 of 8 captured 1987 live through 1989-90, 2 of 11 captured 1988 live through 1989-90, 1 of 6 captured fall 1989 live through 1989-90.

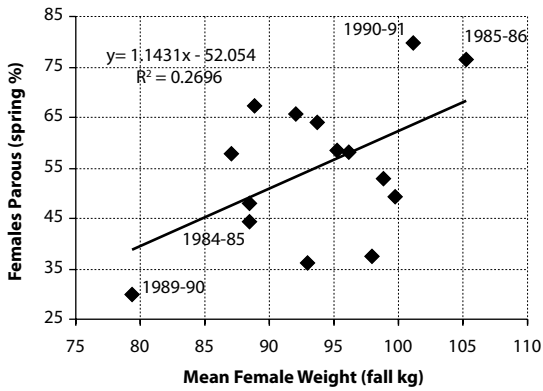


Fig. 4. The significance of the regression of the percent of females classified as parous in the spring on the mean weight of females the previous fall (inclusive of long yearlings) ($r=0.5193$, $df=13$, $P<0.05$) is carried by extreme observations but the conditions leading to them occurred twice in the course of the study. The winters of the most severe starvation events (Fig. 2), 1989-90 and 1984-85, with respectively the lowest and low weights entering the winter and lowest and low percentage parous the following spring, was followed by recovery over-summer of the surviving cows to record weights, and the highest percentages parous throughout the study those following springs. The mean fall sample size, females weighed, was 7.1 ± 0.84 .



Fig. 5. The greatest winter loss of Slate Islands caribou from starvation was in 1989-90. Only 23 tagged animals lived, of which 21 had ages established (Lived), and the survival of adults was only 12-15%. Forty four carcasses (Died) were recovered inclusive of tagged and untagged caribou. Of the animals that lived the 4 and 5 year olds seemed to have a particular survival advantage; these were animals with experience with the landscape, were not investing in reproduction (pregnancy in females, rut and antlers in males; two surviving males were hummels), and were not investing significantly in body growth.

We located eight dead caribou killed by wolves 1994-95. The mean survival of males over the course of the study was the same as for female 82% (320/392, $n=$, 16 years). But unlike the females, they had high survival in both winters when wolves were present 1994-95, 87% (33/38) and 1995-96, 91% (52/57).

The sex and age composition of the animals that we located that died over-winter from starvation (1974 to 1993) was 24 female calves, 18 male calves, 25 calves (sex unknown), 62 adult females, and 77 adult males. The large antlered males died at higher rates than males with smaller racks. The mean pedicel size of males that died in the 1984-85 die-off was 1379.2 ± 261.65 mm² ($n=9$) compared to the random brown/brown antlers cast in the previous fall, 790 ± 195 mm², $n=6$ (measured width x length). Older animals had higher mortality rates also in these die-offs. In the 1984-85 die-off, the mean age of adults captured in the fall was 4.4 ± 0.48 years ($n=15$) and those found dead the next spring 7.5 ± 0.29 years ($n=23$).

The age structure of the dead and survivors was compiled for the major starvation die-off of 1989-90 (Fig. 5). Larger males and older animals that died more than younger caribou were probably investing less in reproduction. Only 7 tagged males survived this greatest winter loss (1989-90) and two had been hummels in earlier years. Generally hummels older than yearlings represented about 5% of the adult male population. On the females side, of 15 tagged

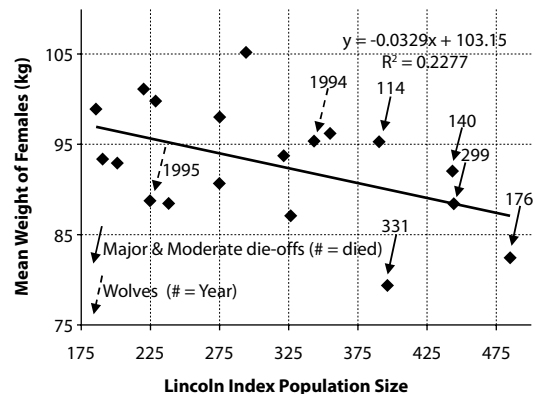


Fig. 6. There was a relationship between the size of the population entering the summer and the mean weights of females that fall ($r=-0.477$, $n=19$, $df=17$, $P<0.05$), indicating a density dependant interaction with summer forage. Die-offs in the following winter were mapped to these data (solid arrows). When the population was in excess of 390 caribou entering the winter, Lincoln estimate, a die-off of moderate to major proportions took place.

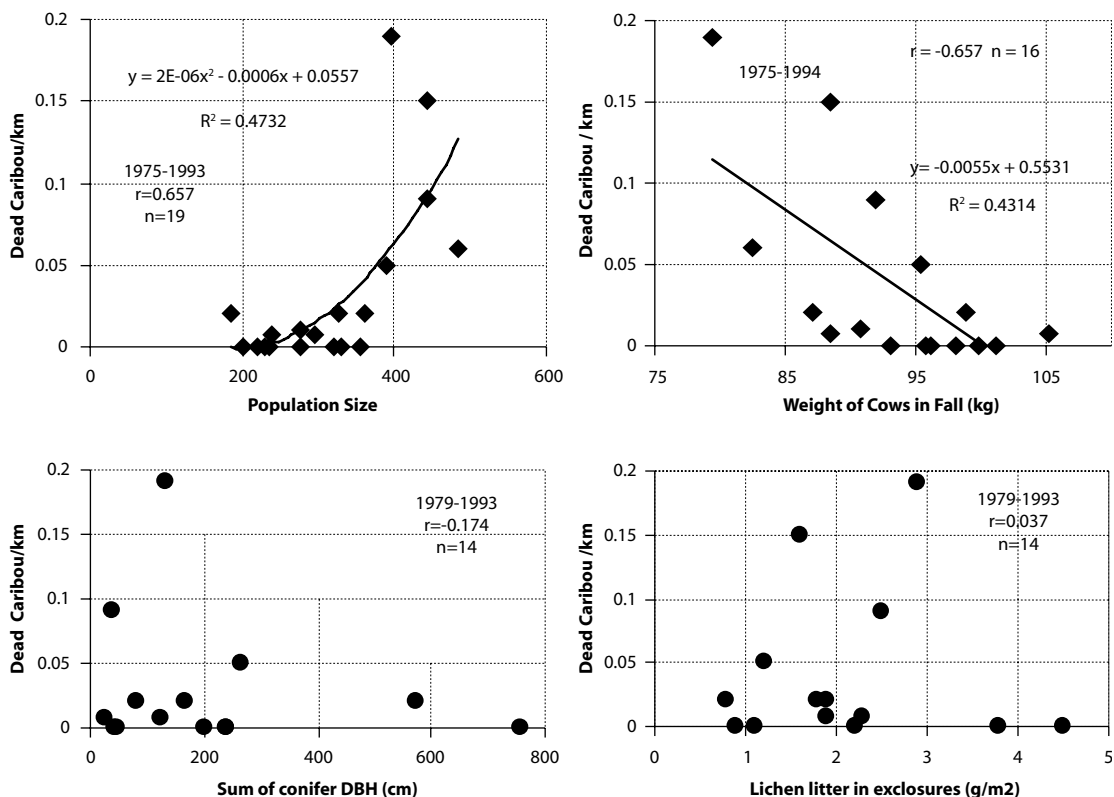


Fig. 7. Starvation die-off events (the number of caribou carcasses located on 'King Census' strip transects walked in May and June each year) were correlated with the Lincoln Index population estimate the previous spring ($df=17$, $P<0.01$), and low weights of female caribou the previous fall ($df=14$, $P<0.01$), and not with the abundance of the total over-winter lichen litter (picked clean from wind blown branches and trees in 6 caribou exclosures each spring), or with the frequency of over-winter conifer blowdown (total diameter at breast height of all conifers fallen over a trail each winter).

females surviving the crash of 1989-90, nine had not been pregnant (no udders seen) and only 6 survived that had borne calves. The oldest tagged animal that lived through that crash was a female we called Hope. She had carried her radio collar (radio signal was lost years before) since 1982. She may have had only one calf in 12 years but she was a survivor, living through 4 winters of moderate to major mortality events between 1983 and 1990 (Fig. 3), when she was 11. She had the largest home range of any of the animals we radio tracked.

The regression (Fig. 6) of fall weights of females on the spring Lincoln Index population estimates ($Y = -0.0329x + 103.15$, $R^2 = 0.2277$) indicates that population density is a predictor of winter survival ($r = -0.477$, $n=19$, $df=17$, $P<0.05$).

The population declined when the fall population exceeded 450 animals ($12.5/\text{km}^2$) and animals died over-winter (Figs. 3, 6). This winter mortality was not correlated with the abundance of winter lichens,

but with the previous years population estimate ($df=17$, $P<0.01$) and fall weights of female caribou ($df=17$, $P<0.01$) (Fig. 7, Table 7). This is our evidence for density-dependent population regulation based on the abundance of green summer forage. After the die-offs, the fall weights of the females increased dramatically the following year in at least three of the die-offs (Fig. 8), in two of those cases the post-die-off population density was low enough that female condition improved sufficiently over-summer to generate a parous percentage the following year which is considered the norm for caribou, the only two times this occurred in the study. The difference in weights between these two years and the third, also a number of other years (Table 7), was small and indicates a threshold was achieved.

Wolves preyed on caribou from their ice-crossing in winter 1993-94 until late March 1996. In the 2 years these wolves hunted, calf survival to October dropped from 10% to 25% in years without wolves

to 5% or less (Fig. 3). The caribou population dropped in the winters of 1994-95 and 1995-96 (Figs. 3, 6) with wolves present and when the caribou population was below the density where starvation events were observed (Figs. 3, 6).

Between March and May 1996, one wolf disappeared and there is some evidence that poison had been deployed. At that time a dog accompanying tourists to the Slate Islands went into fits and was rushed to

a veterinarian; it had ingested poison. After this there was no sign of wolf predation until 2003 and 2004 (Fig. 3). One wolf did persist after the poisoning incident as there was sign near and at a (former) fox denning site in the vicinity of Horace Cove until 1999. If this animal did prey on caribou it was not effective at a level that we could detect demographically or during surveys and the caribou population built up (Fig. 3).

Table 7. Pearson correlations¹ of overwinter caribou mortalities² located per km walked in May/June with: the winter snow depth measured on winter trips; the size of the previous years population (spring Lincoln Index); the lichen litter fall in 5 exclosures of total area 152 m² measured in May; and the total DBH of conifers that fell across a 1.7 km trail overwinter. Also, the correlation of the size of the previous fall population with the mean weight of females the previous fall, and exclosure lichen with total DBH of conifers across the trail.

Winter Season ³	Previous Spring Caribou Estimate	Previous Fall Weight of Cows (kg)	Winter Trip (mo/da)	Depth of Snow (cm)	May/June Walks (km)	Over-winter Mortality (Caribou/km)	Exclosure Lichen/ m ² (gm)	ΣDBH Conifers on trail (cm)
1973-74	----	----	3/7, 3/20	58	99	0.060	----	----
1974-75	----	----	3/11-4/4	62	105	0.040	----	----
1975-76	275	90.7	3/28	69	80	0.010	----	----
1976-77	485	82.5	no trip	----	169	0.060	----	----
1977-78	229	99.8	3/6-21	66	65	0.000	----	----
1978-79	186	98.9	3/18-4/2	85	130	0.020	1.9	165
1979-80	201	93.0	3/20-26	81	101	0.000	1.1	48
1980-81	326	87.1	3/24-27	25	162	0.020	0.8	81
1981-82	238	88.5	3/15-19	75	140	0.007	1.9	122
1982-83	275	98.0	3/21-24	57	133	0.000	0.9	41
1983-84	390	95.3	no trip	----	83	0.050	1.2	264
1984-85	444	88.5	3/18-22	49	158	0.150	1.6	----
1985-86	294	105.2	3/31-4/5	50	154	0.007	2.3	25
1986-87	355	96.2	no trip	----	62	0.000	2.2	241
1987-88	443	92.0	3/15-18	83	93	0.090	2.5	38
1988-89	362	----	3/29-31	70	57	0.020	1.8	574
1989-90	396	79.4	3/26-30	60	168	0.190	2.9	132
1990-91	220	101.2	4/2-5	47	135	0.000	4.5	759
1991-92	237	----	no trip	----	40	0.000	----	241
1992-93	330	----	3/21-23	69	55	0.000	3.8	200

¹ Correlation coefficients:

Overwinter mortality vs snow depths, $r = -0.094$, $n=16$ (ns).

Overwinter mortality vs fall population, $r = 0.666$, $n=18$, $df=16$, $P<0.01$.

Overwinter mortality vs exclosure lichen, $r = 0.038$, $n=14$, (ns).

Overwinter mortality vs DBH conifers, $r = -0.174$, $n=14$, (ns).

Fall population vs mean weight of females, $r = -0.568$, $n=15$, $df=13$, $P<0.05$.

Exclosure lichen vs DBH conifers, $r = 0.525$, $n = 13$, $df=11$, $P<0.10$.

² Overwinter caribou mortalities do not include fall rut related mortalities (antlers on adult male skulls) or accidental deaths.

³ In c.Jan. 1994 two wolves reached the islands.

The population declined between 1999 and 2000 based on the strip census (383 estimated in 1999 and 252 in 2000). There could have been a moderate die-off (Fig. 3) but we did not find any over-winter mortalities. The census was made by the most experienced of our crew (LC). However he walked only 22 km, the lowest total in the 30 years (see Table 7). The mean line of sight distance to dead caribou in previous die-offs was $7.6 \pm 1.02\text{m}$ (6 die-offs and 92 carcasses). Less than 1% of the 36 km² of the study area was scanned. If 100 animals died they all could have been missed with such minimal coverage.

In the last two years of the study, 2003 and 2004, there were signs of a wolf on the islands. In both years, we found carcasses that had bones crushed and scattered and found scats. Studies that have continued in 2005 and 2006 have not confirmed a continued presence for this wolf.

High populations of snowshoe hares occurred on the Slates in 1979, 1988, 1995-96, with the mean population estimated at 267 ± 44 hares (27 years), an extremely low density of 7.4 hares/km² with total population extremes of 61 to 813 total animals. However, interviews with the two original light house keepers, whose tour-of-duties together on the islands spanned 60+ years, both indicated higher hare numbers in prior decades. Hares were noted to have, relative to caribou in the late 1970s, more impact on *Cornus canadensis*, *Maianthemum canadense*, and *Trientalis borealis*; furthermore, they slowed the recovery of these species plus mountain maple post-clipping in clipping-recovery experiments (Bergerud, 2001: unpubl. data)

Pukaskwa National Park

The caribou population in PNP appeared to increase from 1974 to 1979 and then decreased (Fig. 9). The increase was possibly an artefact of learning or there may have been population increase in that period. The overall decline per year is $\lambda = 0.97$. Recruitment averaged 16% (Fig. 9) thus mortality would approximate 18-19%. There was a high rate of disappearance of radio caribou; 23%, 6 animals in 26 radio years (1976 to 1988) (Bergerud, 1989). Eleven caribou were found dead between 1987 and 1999 (K. Wade, Warden, pers. comm.) and all but 1 or 2 were thought to have been killed by wolves.

Radio-collaring wolves in the Greater Pukaskwa Ecosystem documented 2-3 of 7 packs operating completely in the Park (Forshner, 2000: Figs. 4-8). The Cascade Lake Pack was centrally located 7 km from Otter Island and would have had the greatest impact on caribou. The Swallow River Pack was the next pack nearest to the shore and 24 km from Otter Island. The studies by Burrows *et al.* (1996), Burrows

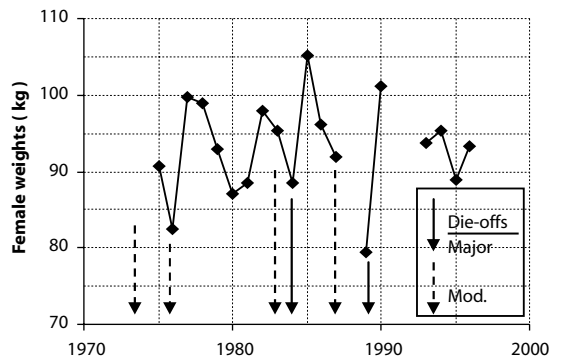


Fig. 8. The fall weights of Slate Island female caribou, and the years of moderate ($100 < \text{mod.} < 200$) and major (≥ 299) starvation die-off events. The weight of females showed major gains in the two growing season observations which followed a major starvation event, and the growing season following the largest moderate event, indicating a density dependant interaction with summerfood resources.

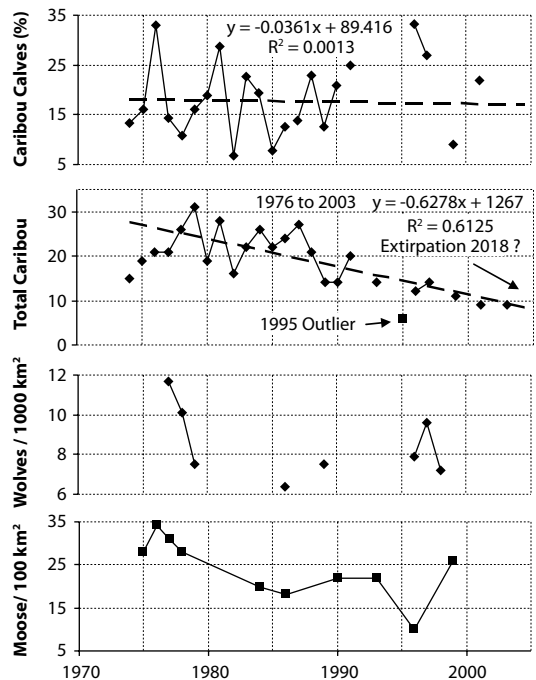


Fig. 9. Pukaskwa National Park moose, wolf, and caribou demographic parameters for the years 1974 to 2003. The percentage calves in winter surveys has remained constant, while the caribou population has declined significantly ($r = -0.783$, $n = 21$, $df = 19$, $P < 0.01$). The trend in total caribou numbers 1976-2003 suggests that extirpation is likely by the year 2018 but below 10 animals a collapse to nil could be imminent, and the chance for the population to cycle up is precariously low.

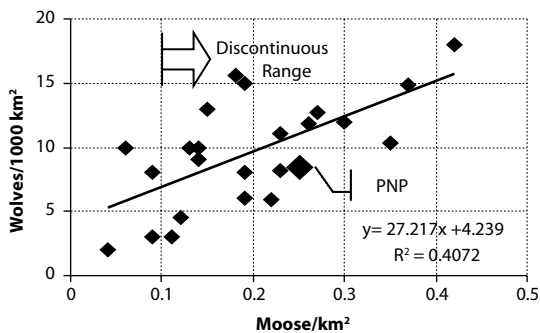


Fig. 10. The regression of wolf numbers on moose densities from published data (Forshner, 2000: Table1-1; Messier, 1994: modified) and updated for Pukaskwa National Park ($r=0.638$, $n=24$, $df=22$, $P<0.01$). Bergerud and Elliot (1986) found that $R=M$ for caribou occurred at 6.5 wolves/1000 km^2 , which in turn is supported by a density of 0.10 moose/ km^2 (Bergerud 1989); thereby fragmenting the continuous range of caribou (i.e. populations persist in isolation or discontinuously where escape/refuge habitat is sufficient to influence R and/or M).

(2001), and Forshner (2000) showed the highest density of moose and wolves was on the north boundary of the Park and even further north where logging was taking place. However three packs probably hunted to the coast. The center of the territory of the Swallow River Pack was 15 km from the coast; the Cascade River Pack had the coast as a boundary and the center of its territory was 12 km from Otter Island; the Black Pack operated adjacent to the shore at Oiseau Bay where the caribou had disappeared by 1988 (Bergerud, 1989).

The wolf population averaged 8.5/1000 km^2 (Fig. 9) or 2 more /1000 km^2 than that predicted for stability in the regression of mortality on wolf numbers of 6.5/1000 km^2 ($n=18$ herds) and recruitment on wolf densities ($n=25$ populations) (Bergerud & Elliott, 1986: Fig. 10 p. 1524). Recruitment averaged approximately 16% when it would be expected to be 9.6% when associated with 8.5 wolves/1000 km^2 ; i.e. $Y=e^{3.340-0.127X}$ (Bergerud & Elliott, 1986). Given that the population was in decline, adult mortality would have been higher than the expected 15.5%; i.e. $Y=4.766+0.669X^{1.275}$ (Bergerud & Elliott, 1986). These differences are most likely attributed to relatively high quality summer refuge habitat and inadequate winter escape habitat. The lake shore distribution and Otter Island provided the escape habitat, but land fast ice along the shore in several winters had provided the access for the wolves and the high winter predation rate. The PNP wolf population size (Fig. 9) was within variation expected based on an estimated

density of moose of 0.25 moose/ km^2 versus that predicted from a regression of wolves on moose densities in other studies (Fig. 10). Burrows *et al.* (1996) had projected the expected number of wolves in the Park based on a density of 0.25 moose/ km^2 at 15 wolves or (8/1000 km^2), close to the mean population estimate over the years (Fig. 9).

There was considerable variability in the methods used to estimate the wolf and moose populations and probably numbers of both species were relatively stable as suggested by Burrows (2001). The low moose count in 1996 may be due to weather causing tracking problems (Burrows, 2001). There is no hunting of moose in PNP and Bergerud *et al.* (1983) argued that moose numbers were regulated by wolf predation, a view rejected by Thompson & Peterson (1988).

The introduced herds

(1) In 1982, 7 animals were move onto Michipicoten Island to add to the one resident male which had been seen on the island: transplants - 1 male, 3 adult females with 3 female calves. An eighth transplant, a male, was added in 1989. The island is 188 km^2 and 15 km off shore. The Island is in the Great Lakes-St Lawrence Forest Region (Rowe, 1972). The dominant trees are all maples, mountain maple, sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*) plus birch and aspen. Ground hemlock and white pine (*Pinus strobus*) are common and there are some boreal conifers on one ridge. The herd increased $\lambda = 1.18$ (8 to ± 200 , 160 counted in 2001) in 19 years.

(2) Ten animals were moved onto Montréal Island by 1984. The Island is 7 km^2 and 5 km from the coast. The island is mostly boreal forest of spruce, fir, and birch with terrestrial lichen common on only one sandy point. The caribou increased to approximately 20 animals by 1993 (16 seen). In 1994, when Lake Superior froze, wolves reached the island predating some and causing the balance to abandon the island.

(3) Seven animals were released on Bowman Island in 1984, in the complex of islands commonly referred to as the Rossport islands of Lake Superior (access from Rossport, Ontario). The island is adjacent to St. Ignace Island where the last caribou were seen in that vicinity in the 1940s (de Vos & Peterson, 1951). The forest cover on the island is mostly boreal forest. All the animals had radio collars. The animals disappeared by 1986. Two caribou were found killed by wolves. It is believed the others were killed on the ice in bays and channels of the Rossport islands and their collars lost (divers attempted to recover collars but the collars were not a suitable frequency for accurate underwater triangulation). The last animal alive had moved further off the coast to a small island suggesting movement to escape habitat.

(4) Thirty-nine animals were moved into Lake Superior Provincial Park in the fall of 1989. This park is in the Great Lakes-St. Lawrence Forest Region and forest cover is similar to Michipicoten Island. By June, only 1 of the 17 radio collared animals was still alive. On investigation, the majority of the carcasses had been utilized by wolves, and were either killed or scavenged by them. In retrospect, the animals moved from the Slates Islands had extremely low weights in October 1989, some of the released animals that died probably could not respond adequately to encounters with wolves. However this release has persisted in the escape habitat of the coast and a survey in February 2007 found three animals, the herd numbers less than 10 animals and is decreasing (biologist G. Eason, pers. comm.).

Discussion

Slate Islands forage resources

We observed that snowshoe hares did compete for summer foods with woodland caribou on the Slate Islands, and while not directly relevant to the competition for forage, the effect of hares was most noticeable in the limitation of white spruce recruitment. The latter may have implications for plant community succession. Specific calculations of the magnitude of hare competition for forage were not carried out. From observations of exclosure experiments (unpublished) and permanent vegetation plots (unpubl.), it was evident that hares were out-competed by the massively larger total biomass of woodland caribou.

The prime example of caribou out-competing hares was salmonberry/thimbleberry (*Rubus parviflorus*); green terminal canes were preferred by hares and essentially 100% were cropped each winter. In 1978, the mean height of the highest live bud ranged from 61.5 cm to 83.0 cm on four permanent plots where thimbleberry coverage was 100%. However, there was no qualitative difference between the height this plant achieved each summer and mainland examples until the mid-1980s. At the outset of studies, thimbleberry was lightly used as summer food by caribou with most use noted on emerging leaves and a noted lack of preference for mature leaves; this plant swamped caribou use. With the combination of functional extirpation of more highly preferred caribou summer forage species and extremely high caribou densities 1985 to 1989, caribou also consumed this species as a summer food. In a matter of a few years it was eliminated islands-wide from functional utility. Up to that point, thimbleberry had been very common in continuous large patches (100s of m in extent); after, the only place we could show this plant to visitors was in exclosures. The story is similar for other plant

species but not so dramatically unambiguous. For the purposes of any conclusions drawn, the hares were considered to have a negligible impact on caribou population dynamics, or in contributing to the functional depletion of plant species.

The lengthened growing season documented for the Slate Islands, where spring green-up had advanced by almost a month from 1967 to 1988, seemed to maintain if not continue in later growing seasons. Plant phenology was closely monitored in the late 1970's and in the more recent years casual observations confirm by comparison that early green-up has continued. If all else were equal, this longer growing season would mean that plants garner greater energy reserves and this benefit would pass on to herbivores. This may not be the case where over-grazing is occurring. The opportunity to swamp herbivores with biomass and thereby allow a larger net seasonal energy gain per individual plant may be greater in a shorter growing season. A longer growing season, and larger energy transfers to the higher trophic level, might therefore accelerate the functional extirpation of plant species from the Slate Island plant communities.

The importance of energy retention at the plant level is very high. While energy transfers between trophic levels were not studied intensively in this study, we realized in time they should have been. When plant studies were initiated in 1977 on the Slate Islands (WJD), it took some time to realize that a number of *unknown* species were actually diminutive forms of common boreal forest plants. It was assumed at first that this was a localized climatic effect, in which the cold thermal mass of Lake Superior interacted with the off-shore location of the Slate Islands to thwart normal growth; that is, as seen in forest communities on the adjacent mainland. Mainland plant forms were typical of the plants throughout their range. Exclosure plots showed overgrazing depleting energy resources; plants survived in small form and at low density making them less a target for concentrated foraging. A capacity to sprout from extensive root systems was essential to this plant survival strategy. The following example is illustrative of what occurred for all the most highly grazed plant species including Canada mienthemum, starflower, big-leaf aster, and others which were available when our studies began. Clintonia, already described as being present only as specimens with single 10 cm or less leaves and not producing flowers when studies began, was present in a number of exclosures when they were erected. With each year that passed, the size of the leaves produced was more elongated; after a few years plants started producing second leaves as is their normal form, and then after 5-7 years, clintonia in exclosures would flower; and would do so each

year thereafter. The importance of retained/retrieved energy in the root systems for these perennial plants is apparently critical to their presence in what is considered a normal form throughout the extent of their ranges.

Mountain maple stems in the forest sub-canopy, safe from browsing, have been harnessed by woodland caribou as nutrient pumps. The typical maple sucker gardens described earlier formed a very large portion of the summer forage available throughout the 30 years of this study. Normally, mountain maple is restricted to the understory and in a shrub form because vigorous suckers originating on the root ball in close proximity to the growing stems share and then fully acquire apical dominance. The suckers then out-compete larger stems and cause senescence and death of stems 2-4 cm diameter, and so normally restrict maximum stem age to 10 to 15 years of age. The overgrazing refuge form of mountain maple is 6-15 cm diameter stems reaching sub-canopy tree status and up to 50 years old. This is not a secure refuge in the time dimension as the trees will not live forever, but due to their shrub nature they have the ability to fill canopy openings with recruits, if they escape caribou browsing. The age distribution documents stem recruitment at low rates peaking in 1947. That this was a low rate is supported by the presence of older stems which would have been lost in whole to the apical dominance effect of being swamped by oncoming sprouts. Recruitment to the canopy has been in decline since 1950, was weak in the 1960s, and ceased altogether c. 1971 (Fig. 2). cursory examination of the age distribution of sampled maple stems (Fig. 2) suggested that senescence mortality might set in for stems between 25 and 35 years age and be progressive (j-shape) through to age 50. Recent observations confirm that the maple sub-canopy is in serious senescence decline. Although the stands sampled did have some dead and dying stems in 1978-82, the health of those stands was still generally good and the forest floor was not littered with a steady accumulation of rotting maple stems. Also, the maple stands are outliving the predicted timeline for senescence decline. Only about half of the stems that should be dead by now according to the senescence theory are actually dead (ocular estimates WJD). Given the age of the stands and what would have been early competition for canopy space with tree species, the 1929 date for initial stems entering a sub-canopy position might correspond to the availability of this niche forming in those stands. It can be said, however, that the senescence that has set in has compromised the health of the sucker gardens too and so the energy transfer to caribou is undoubtedly in serious decline.

By virtue of the retention of a record of foraging intensity across a half century, the mountain maple tells us a lot about this caribou population. After the 1989-90 die-off when the caribou population recovered slowly from a low of approximately 100-200 caribou, the maple took full advantage and sprouts attained heights of 1-2.5 m before the population of caribou were able to catch up and kill these. For all intents and purposes, none of these sprouts have made their way into the canopy, possibly an escapement in the order of the 1971-72 escapement but we think less in fact. This sequence happened at a time when senescence was showing up in the sprout gardens and when most other forage plants were severely depleted or functionally extirpated. Earlier maple ingress into the sub-canopy was not occasioned by such severe coincident conditions; extrapolating the density that caribou were at in the past when maple escaped cannot be done directly from the 1990 case because the overall foraging situation was different. Maple escapement was probably possible in the past at the same or higher caribou density than that which fully suppressed it in this case. Whatever the fine details, the maple age record, and our caribou population monitoring since 1974, clearly document that caribou have been able to control the escapement of maple since at least c. 1930 on the Slate Islands. The absolute quantity of area in which maple occupied a sub-canopy position in those establishing stands is unknown, but it was extensive as indicated by the similarity between the four sampled stands, but still the interaction of caribou numbers with that resource is unknown. With good confidence we do extrapolate from the maple record and its current distribution that the mean population has been maintained at or above an average of approximately 200 caribou since 1950 at a minimum. Before that we know that caribou numbers were consistently high with respect to the available maple resource back at least to c. 1929.

Slate Islands population demography

Over the years we've encountered some persons (scientists, wildlife managers, and forest managers) who brush off the Slate Islands as not being able to seriously contribute to the debate on limiting factors for woodland caribou - they are islands and therefore different; we assume an impression from the theory of island biogeography that populations on islands are known to go extinct at higher rates than mainland populations is at the root. To us this is more correctly an opportunity to understand the species biology in extreme evolutionary conditions, and thereby such studies contribute to understanding the true limits to phenotypic and genetic plasticity of the species. This becomes a reality check against which all other conclusions

about the species in other habitats must be considered. That is, if an assertion is not true in a natural experiment with pseudo-controlled critical variables, then it cannot be true in other circumstances. Any population that persists does so by producing sufficient recruitment and avoiding excessive mortality; observations of different behavioural tactics between ecotypic populations (Mallory & Hillis, 1998) which solve for mean $R=M$ population viability over time do not falsify this truth.

The Slate Island population has persisted for 70+ years on an island archipelago in the absence of predators and in the absence of sufficient lichen for the maintenance of health in seemingly most if not all winters, and in periodic winters the population suffered outright starvation of moderate to large proportions. In 1949, in a period when winter availability of arboreal lichen litter-fall and tree blow-down would have been relatively negligible compared to our studies initiated in 1974, caribou browsed deciduous browse in the fashion of white-tailed deer or moose (*Alces alces*) (Cringan, 1956). This behaviour was not observed in our studies presumably because deciduous browse availability was approaching nil, or the species still available were not preferred.

In this study, females achieved pregnancy rates that are normal for caribou only in 1985 and 1990 when they weighed 100-105 kg the previous fall (Fig. 4). Cameron & Veer Hoef (1994) concluded that small shifts in mass distribution result in relatively large changes in parturition rates. Our results indicate a set-point weight for the Slate Islands that can be achieved following starvation in one growing season; with a major reduction in total caribou numbers, a female can reach her set-point in the next growing season. In June 1990, females averaged 83.6 ± 3.26 kg ($n=11$) and three months later their mass was 101.2 kg resulting in 80% parous in 1991. Thus major increases in parturition rate in 1986 and 1991 occurred with major changes in mass (Figs. 4, 8). Winter forage conditions did not mitigate this rate; if winter forage would have, there was an expectation for other years that females entered winter in almost as good condition, and where die-offs did not occur, to have witnessed a high parous rate too. With animals dying over-winter, with survivors recovering on over-grazed range and starting from the worst possible body condition, in one growing season they achieved the normal pregnancy rate for females (Bergerud, 1980). It appears that a major adaptation of caribou to summer food shortage is to skip reproduction for the following year. The physiology of skipping was not investigated in this study but the small body size of younger cohorts and low average fall weights of adults suggests failure to ovulate.

The average deviation in the population estimates 1974-1992 is 38% of the mean estimate whereas from 1993-2003 it was 13.5%. There was a shift in stability in the population when the wolves arrived. This shift is not fully attributable to wolves since they were not present consistently through the period. They may have reversed an increase in the population that may have been shaping up when they first arrived in 1994 thereby stabilizing the population for 2 to 3 years in the relative sense, but the increase in caribou numbers continued after detectable wolf predation stopped in early 1996. The wolves left a footprint in the age structure of the living caribou that may have had a ripple effect on productivity as the impact of two missing cohorts (1994 and 1995) advanced through the population.

The second factor that has changed is the increase in the abundance and age of the conifer forest cover types. Two tree pathologies are present in abundance on the Slate Islands and interact with this increase in age and abundance of the conifers: armillaria root and butt rot is widespread making stems vulnerable to breakage and trees to wind-throw in windstorms; and spruce budworm although present and causing light damage earlier, was causing heavy tree mortality in the later years. Both the litter and dead fall indices 1979 to 1993 were positively curvilinear when plotted against year (Bergerud, 1996: Fig. 3).

The caribou of the Slate Islands are a good example of the "maintenance phenotype" (*sensu* Geist, 1998). The females are small bodied, the smallest of 21 populations (Butler, 1986: Fig. 11.12 p. 490). Yearlings do not reach puberty, nor do 2 year olds (Bergerud, 2001). Male and female antler lengths are the least of 17 populations (Butler, 1986: Fig. 11.10 p. 487). Again dimorphism is least on the Slate Islands of 30 populations (Butler, 1986: Fig. 11.7. p. 479). Maternal females and their calves are often apart; udder sizes at calving do no approach the size seen in other herds; males were also smallest of 19 populations; and antlerless males ("hummels") occur and do not grow any antlers until 3 or 4 years of age (and then they are diminutive) (Butler, 1986). The antlers of males have gotten smaller over the past 50 years (Bergerud, 2001). This maintenance phenotype enables them to persist in this food limited environment.

Pukaskwa National Park

The caribou population now appears headed for extinction. The count in 2007 was 5. For the interval 1974 to 1988, the dynamics suggested that wolf predation was density dependent (possibly chance encounters involved) (Bergerud, 1996: Fig. 3). Recruitment declined when numbers increased beyond 20 animals and adult mortality increased. Stochastic

factors of snow depths and land fast ice were also considered to affect the contact rate between wolves and caribou. Bergerud (1989) had argued that the moose moved toward the Lake Superior shore in winters of deep snows increasing the presence of wolves. This directional movement was not supported by radio tracking 35 moose in two years (Burrows, 2001). The moose did make summer-winter movements, but they were mostly north and south, shifting to denser forest cover in winter and more deciduous in the summer. The second stochastic factor that should still be valid was the presence of land fast ice that allowed the wolves a lakeshore highway and sometime access to Otter Island (Bergerud, 1989). One counter-intuitive observation of a plus for caribou survival is that with climate change warming the area, the chance for shore-fast ice decreases. But the new negative is that the remaining animals are few and now concentrated in the vicinity of their key island. If the wolves in the two nearby packs had satellite collars that reported daily, a warden stationed at Otter Island could be alerted when wolves approached the shore and if land fast ice was present might possibly turn the packs back inland. Parks Canada has a splendid record of supporting research of this moose-caribou-wolf system and their endangered mammal. Caribou in the Park may have a chance until that day, which is coming, when white-tailed deer arrive and occupy the low snowfall belt along the Superior shore.

In summary, on the Slates Islands we studied an aging ecosystem which has been extensively modified by ungulate inhabitants, and pathologies in the forest canopy. Throughout seventy plus years, the population appears to have been primarily limited by summer food supply affecting over-winter survivorship and parous percentages with occasional stochastic interference by winter weather nudging the survivorship probabilities in either direction. The brief tenure of two wolves demonstrated the vulnerability of caribou to high wolf density. The potential for future persistence seems positive. In contrast, in spite of abundant food in all seasons, the caribou of PNP show little hope of future existence due to being flanked by healthy breeding wolf packs supported chiefly by moose as prey, and the threat of the arrival of white-tailed deer. Implementing the second stage of the crucial experiment on Michipicoten Island before caribou forage is over-grazed would buttress the less controlled examples of the Slates and other introductions which indicated that ecosystems without predators are limited bottom-up by food and those with wolves top-down by predation. The views in 1974 that predation was not regulatory has in most minds been laid aside, we have made some progress.

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